THE ROOT-HAIRS, CAP, AND SHEATH OF AZOLLA.

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(WITH PLATE XVI)

ROOTS spring from the prostrate floating shoots of Azolla in acropetal succession at the points of branching. They are from 2 to 5^{cm} in length, undivided, slender, and delicate, and in *A. filiculoides* and *A. caroliniana* are often, perhaps generally, provided with long outstanding hairs. These trichomes are peculiar in that they originate in the immediate neighborhood of the growing point, and from the first are marked out as cells designed for a distinct office. The way in which the hair initials, or fundaments of the root-hairs, are cut off, and the specialized character of the mature structures have not been described, so far as I am able to learn.[1] The material of *A. filiculoides* upon which Strasburger chiefly founded his classical memoir, "Ueber Azolla," presented a condition of the root quite unlike that which I have found in the same species. His plants had the roots enveloped in root-sheaths, and must have been entirely destitute of the trichome structures which form the principal subject of the present account. My own plants were somewhat variable, the roots occasionally being devoid of hairs. Yet the three lots of living material from independent sources which I have been able to see all exhibit the interesting process of hair formation to be described.

THE SHEATH AND CAP.

As the root-sheath and cap in the plants studied do not entirely conform to Strasburger's account, I shall take occasion to note the points of difference. For the sake of completeness Strasburger's exposition of the origin and early stages of the

[1] Several references to the existence of these trichomes and one account of their peculiar distribution are to be found: WESTERMAIER and AMBRONN, Ueber eine biologische Eigenthumlichkeit der *Azolla caroliniana*. Verhandl. Bot. Verein. Provinz Brandenburg **22**: 58. 1880; BERGGREN, S., Om Azolla's prothallium och embryo. Lunds Univers. Årsskrift **16**: 1878–1879.

root may be briefly recapitulated. In illustration two of his figures have been reproduced (*figs. 1, 2*).

The root of *A. filiculoides* begins with the differentiation of a large cell near the recurved tip of the growing stem beneath, at one side of the median plane, and in close proximity to an incipient lateral bud. This cell is the root initial (*fig. 1*, RI). It abuts internally upon cells from which later the vascular system of the stem originates. It is covered externally by a tabular cell, the root-sheath initial (SI), which subsequently divides once periclinally (*figs. 1, 2*, S, S^1), and eventually in other directions. While at the very first the sheath is thus two-layered, the inner layer very soon disintegrates, and the mature sheath is only one cell thick. As stated above, this sheath in the condition of the plants seen by Strasburger envelops the root completely, though loosely, throughout life.

From the root initial (RI) a pyramidal apical cell is organized (*fig. 2*, AC). A single cap cell is cut off (CI), which afterwards, according to Strasburger, divides but once periclinally, a two-layered, adherent cap thus being instituted.

Fig. 3 of the accompanying plate represents a very young root. It is enveloped by a sheath comprising a single layer of cells. Shortly after the stage shown, this sheath in all the cases seen by me ceases to grow, and the root, continuing to elongate, bursts out. The old sheaths are to be seen as short collars, less than a millimeter long, around the bases of the roots.

The cap, as seen in *fig. 3*, is composed of two very similar cell layers (C^1, C^2). In roots slightly more advanced a sharp differentiation of these layers is seen to have taken place. The outer becomes radially thicker, and its cells are vacuolated; while the inner remains relatively thin, and its cells are well filled with contents staining heavily like those of the body of the root. These differences forecast the very unlike histories of the two layers at a period a little later still, when the outer one, no longer growing longitudinally, becomes detached from the stem at the root's base, and being loosened from the root except at the tip is borne as a distinct cap; while at the same time the inner continues to grow and remains in connection with the root

trunk, like an epidermis (*fig. 4*, c²). After the root is about one-fifth grown the inner layer develops no further and is torn away at the base, to be carried downward as a cap in the further growth of the root, the upper part of the trunk therefore being left naked.

It may be worthy of remark that in its younger stage the root of *Azolla filiculoides* thus presents a state of things analogous to that in typical dicotyledons, since the superficial layer of the body of the root is derived from the calyptrogen — if we may so speak of the original cap segment (c1); whereas the mature root is like that of other vascular cryptogams and monocotyledons among flowering plants in exposing an unprotected cortex back of the root-cap.

In all cases examined by me there is an extra periclinal division at the apex of the inner cap (*fig. 4*, d).

In *Azolla caroliniana* I find that sheath and cap behave as stated for *A. filiculoides*, except that the second periclinal division (d) is absent.

THE ROOT-HAIRS.

In the majority of vascular plants root-hairs are formed by the external cells of the root in the region which is ceasing or has ceased to grow, where cell-division has been suspended and the tissues have become fixed. Here any or all of the cells without distinction of form, size, or contents may send out the organs of absorption. Only one exception was known to DeBary, that of Lycopodium, where the hair initials are set off in the still plastic epiblema not far behind the apex, and these, remaining short while the intervening cells elongate, alone produce tubular outgrowths. For the sake of comparison a figure of these hair initials and of the resulting structure in *Lycopodium lucidulum* is given (*fig. 11*). De Bary overlooked Bruchmann's observations[2] on the production of root-hairs in essentially the same manner in Isoetes, by the early establishment of special cells for the purpose.

The initials of the trichomes in the root of *Azolla filiculoides*

[2] BRUCHMANN, H., Ueber Anlage und Wachsthum der Wurzeln von Lycopodium und Isoetes. Jenaische Zeitsch. Naturwiss. 522. 1874.

(*fig.* 4, TI) arise within a belt of actively dividing cells, lying immediately under the inner root cap, not far from the apex, at an actual distance varying with the rate of growth of the terminal region. When that growth is most rapid the longest space intervenes between the apical cell and the youngest hair initials. As the root reaches the limit of its development, the hair-forming impulse travels downward until the apical cell itself is split into several parts, each one piliferous. The initials are formed in zones or partial zones. The mitoses to which they owe their existence are peculiar in that the axis of the mitotic figure in each case diverges more or less from the longitudinal axis of the mother cell, so that the resulting cell plate and wall lie somewhat diagonally (*figs.* 4, 8). Division thus gives two more or less wedge-shaped elements, of which the lower and slightly larger one is the hair initial.

This cell never elongates much in a direction parallel to the length of the root. The tube, which presently begins to grow out, turns toward the root apex (*figs.* 5, 6). As the hairs lengthen they at first lie appressed to the root and may be seen confined by the inner cap, which is now distended and pushed away from the root trunk (*fig.* 9). The whole cap structure is finally thrown off through the growth of the lower hairs, and the hairs themselves stand out strongly (*figs.* 12, 13). Their bases retain the wedge-form of the original hair initial.

Soon after their organization the hair initials are to be distinguished from the cells with which they alternate by their contents, no less than by configuration, since they are more richly supplied with protoplasm (*fig.* 5).

The lesser wedge-shaped cell produced simultaneously with the hair initial elongates and soon divides transversely (*figs.* 6, 9) once, twice, and often three times. The trichomes in each longitudinal cell row thus become separated by two, four, or eight cells. The intervening cells may be six, however. The number of divisions in neighboring rows may be different; and through the resulting displacements the original regularity of the hair zones is destroyed.

In the root of *A. caroliniana* the differentiation of the trichomes proceeds as in *A. filiculoides*.

The full grown hair may attain a length of about 2 mm. Its short base and the position with respect to the other elements of the epiblema, which it occupies in consequence of its peculiar origin, give this sort of trichome a distinctive character (*fig. 10*). The fact will be appreciated upon comparison of the figures accompanying these notes with the root-hairs of ordinary dicotyledonous plants.

The superficial layer of the root trunk in *A. filiculoides* and *A. caroliniana* may be described as usually comprising, apart from the apical cell, four regions. Beginning with the youngest, these are: (1) a region of embryonic tissue in which the divisions are equating divisions; (2) a short zone where the divisions are differentiating divisions, giving rise ultimately to two sorts of members, trichomes and flat or prismatic cells; (3) a more extended belt, in which the cells of the second class again undergo equating divisions, and elongate; (4) a region of matured and fixed tissue, covering the greater part of the root. These regions represent successive stages in the genesis of the layer under discussion. An epiblema with such a complex history is characteristic not only of Azolla—a highly specialized, terminal group—but of wide ranges of fern allies and monocotyledons, and of an isolated group of dicotyledons. My attention was first drawn to the matter by the similarity of Sagittaria and Nymphaea in this respect. I find a similar type of epiblema in many members of Juncaginaceae, Potamogetonaceae, Aponogetonaceae, Naiadaceae, Alismaceae, Hydrocharitaceae, Juncaceae, Cyperaceae, Gramineae, Commelinaceae, Xyridaceae, Eriocaulaceae, Haemodoraceae, Zingiberaceae, Marantaceae, Orchidaceae; and in Nymphaeaceae (Nymphaea, Nuphar, Brasenia, Cabomba) alone among the dicotyledons examined. That the same trait is exhibited by such divergent groups as Lycopodium Isoetes (already noted by Bruchmann), Selaginella, and Equisetum—the last two instances seem to have been overlooked—shows that we have to do with an old element in vascular plants.

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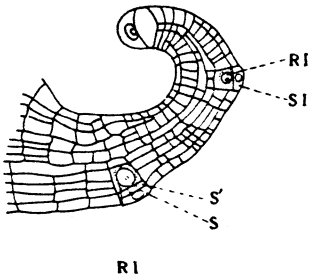

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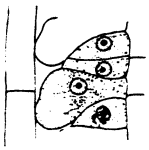

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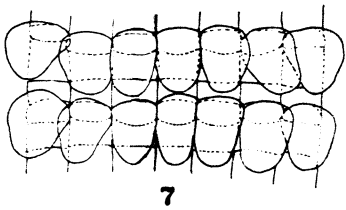

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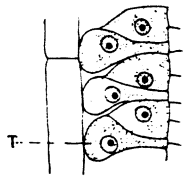

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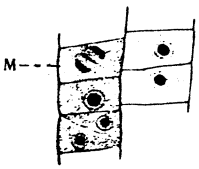

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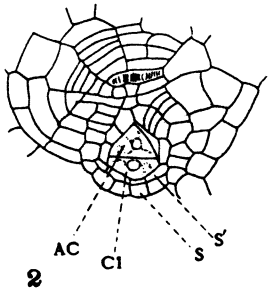

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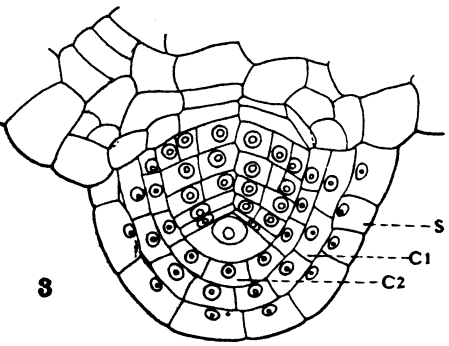

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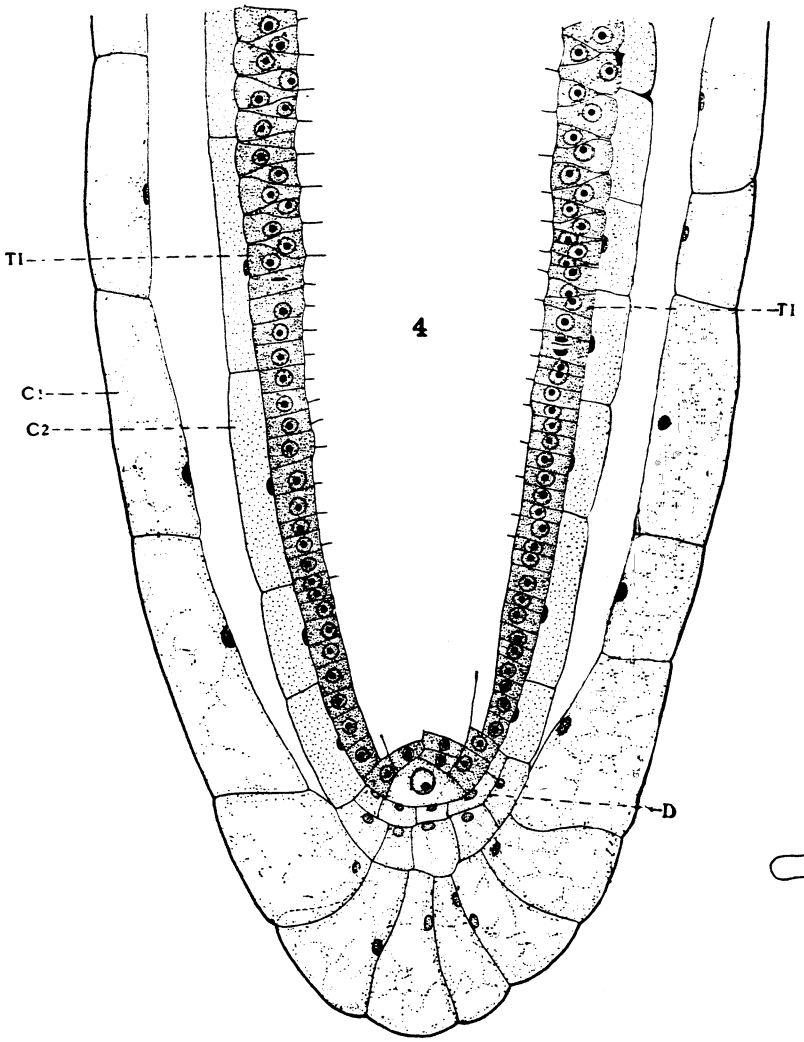

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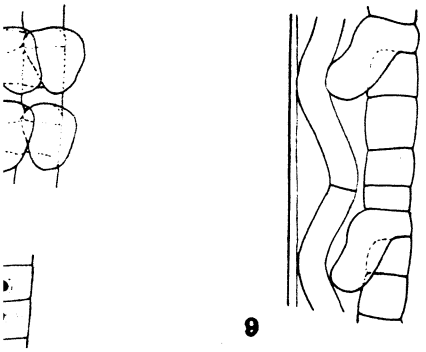
LEAVITT on AZOLLA



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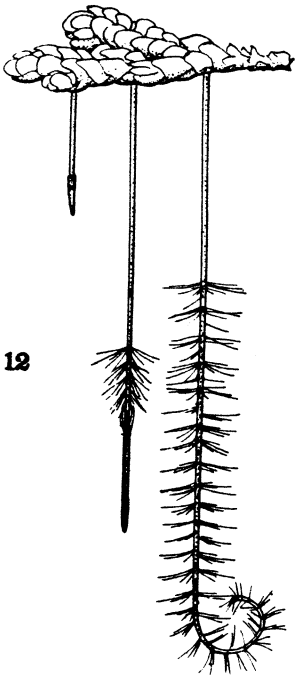

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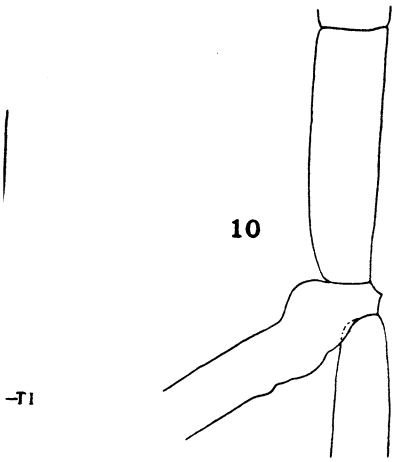

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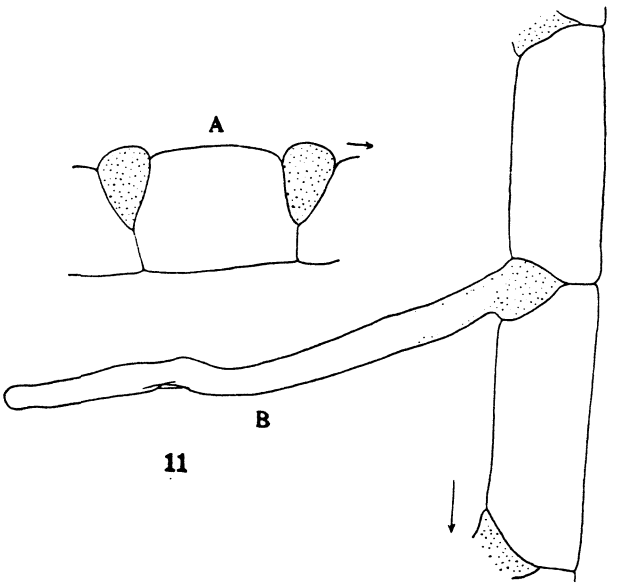

A

B

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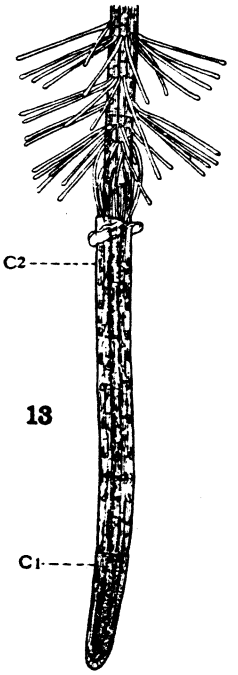

C2

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C1

EXPLANATION OF PLATE XVI.

All figures except *figs. 1, 2, 12*, were drawn with the aid of the camera lucida.

FIG. 1. Longisection of the growing apex of the stem in *Azolla filiculoides* (after Strasburger): RI, root initial; SI, sheath initial; S, S^1, segments of sheath initials; × 260.

FIG. 2. Fundament of the root in the same species (after Strasburger): AC, apical cell; CI, cap initial; S, S^1, outer and inner sheaths; × 260.

FIG. 3. Longisection of a young root of *A. filiculoides*; S, sheath; C^1, C^2 outer and inner caps; × 450.

FIG. 4. Longisection of the growing tip of a root of *A. filiculoides* (microtome section from material embedded in paraffin); D, periclinal division at apex of inner cap; C^1, C^2, outer and inner caps; TI, hair initial; × 450.

FIG. 5. Hair initials and intervening cells at the beginning of the growth of the hairs, about ten cell pairs removed from the oldest shown in *fig. 4*; × 450.

FIG. 6. First transverse division of intervening cell; × 450.

FIG. 7. Young root hairs seen in tangential section of the root, showing zonal arrangement; × 450.

FIG. 8. Origin of the hair initials; close of mitosis and forming cell-plate are seen at D; × 750.

FIG. 9. Young hairs in radial longisection, separated in the row by four intervening cells; × 300.

FIG. 10. Base of mature hair, between elongated epiblema cells; × 450.

FIG. 11. *A*, initials at the edge of the root-cap, and *B*, relatively young hairs near the tip of the growing root of *Lycopodium lucidulum*; the arrow shows the direction of the root apex; × 450. A peculiarity of Lycopodium is that in most species the hair initials usually divide longitudinally, so that the hairs stand in groups of from two to four.

FIG. 12. Habit of *Azolla filiculoides*; × 5.

FIG. 13. Terminal portion of root, showing cap and root-hairs; × 24.